

April 2000

## Variation in Timing and Abundance of Elfins (*Callophrys*) (Lepidoptera: Lycaenidae) in Wisconsin During 1987-1999

Ann B. Swengel

Scott R. Swengel

Follow this and additional works at: <https://scholar.valpo.edu/tgle>



Part of the [Entomology Commons](#)

---

### Recommended Citation

Swengel, Ann B. and Swengel, Scott R. 2000. "Variation in Timing and Abundance of Elfins (*Callophrys*) (Lepidoptera: Lycaenidae) in Wisconsin During 1987-1999," *The Great Lakes Entomologist*, vol 33 (1)  
Available at: <https://scholar.valpo.edu/tgle/vol33/iss1/9>

This Peer-Review Article is brought to you for free and open access by the Department of Biology at ValpoScholar. It has been accepted for inclusion in The Great Lakes Entomologist by an authorized administrator of ValpoScholar. For more information, please contact a ValpoScholar staff member at [scholar@valpo.edu](mailto:scholar@valpo.edu).

VARIATION IN TIMING AND ABUNDANCE OF ELFINS (*CALLOPHRYS*)  
(LEPIDOPTERA: LYCAENIDAE) IN WISCONSIN DURING 1987–1999Ann B. Swengel and Scott R. Swengel<sup>1</sup>

## ABSTRACT

In Wisconsin during 1987–1999, we recorded elfin (*Callophrys*) individuals on 154 of 254 observation dates between 2 April and 11 July. The frosted elfin (*C. irus*) occurred only in central Wisconsin; brown (*C. augustinus*), hoary (*C. polios*), and Henry's (*C. henrici*) elfins in central and northern Wisconsin; and eastern pine elfin (*C. niphon*) from southern to northern Wisconsin. Most individuals were eastern pine elfins, which occurred at the most sites, while Henry's elfin had the fewest individuals and sites. All five elfins occurred in the most frequently visited subregion (central Wisconsin), where they all had similar median and mean observation dates for all study years pooled. For most elfins, the number of individuals observed per year covaried significantly with the span of days between first and last observation dates that year. Within species, mean and median observation dates in the earliest year(s) always occurred before the first observation date in the latest year(s). We compared the phenology of the frosted elfin flight period to the timing of olympia marble (*Euchloe olympia*) adults and spring Karner blue (*Lycaeides melissa samuelis*) larvae and adults. The least variable relationship was the date of first mature Karner larva (typically before first frosted elfin adult, and bracketing that date by only 8 days). Only the frosted elfin showed a significant influence of weather (temperature only) on observed density, while most elfins significantly increased the nearer to noontime. We recorded elfins in broad ranges of weather conditions and daily timing. Elfin abundance fluctuated markedly among years based on the mean of peak survey totals at the same monitoring sites in central Wisconsin each year from 1992 or 1993 to 1999. One "outlier" site each for frosted and eastern pine elfins had much higher peak survey totals than the other sites. Abundance fluctuations in the outlier and other sites did not correlate significantly for either species. For most elfins, the percent sites where the species was recorded as present each year covaried significantly with that year's annual mean of peak survey totals. This indicates that the ability to document presence of an elfin relates to the species' abundance that year. Since elfin abundance and flight timing and length varied considerably among years, the appropriate time for elfin detection must be determined individually for each year and assessments of an elfin's status and abundance cannot be reliably based on surveys at only a few sites or in a few years.

---

Five species of elfins (*Callophrys* Billberg 1820) (Lepidoptera: Lycaenidae) have been recorded in Wisconsin (Opler and Krizek 1984, Scott

---

<sup>1</sup>909 Birch Street, Baraboo, Wisconsin 53913 USA.

1986, Glassberg 1999). They complete one generation per year, with the adult stage occurring in spring. Brown [*C. a. augustinus* (W. Kirby 1837)] and hoary (*C. polios* Cook and Watson 1907) elfins range widely in boreal and montane North America in acidic habitats (bogs, barrens, upland forest edges). In the eastern U.S., they use short shrubby heaths (Ericaceae) as larval food plants. The range of the frosted elfin [*Callophrys i. irus* (Godart 1824)] occurs from northern New England to Michigan and Wisconsin, with scattered populations southeast to northern Florida. This subspecies is known or inferred to use wild lupine (*Lupinus perennis* L.) (Fabaceae) as larval host (Kuehn 1983, Gatrell 1991, Schweitzer 1992, Swengel 1996, Nielsen 1999), a perennial herb of open-canopied habitats on xeric, sandy soil (Dirig 1994). With a range in the eastern U.S. and adjacent Canada, the Henry's elfin [*C. h. henrici* (Grote and Robinson 1867)] uses various flowering shrubs and trees (Aquifoliaceae, Caprifoliaceae, Ebenaceae, Ericaceae, Fabaceae, Rhamnaceae, Rosaceae) as host. Usually only one host is used in an area, and the host(s) in Wisconsin remain unreported. The eastern pine elfin (*C. niphon clarki* T. N. Freeman 1938), which uses pines (Pinaceae) as larval host, ranges throughout the eastern U.S. east of the Great Plains and southern Canada east of the Continental Divide. The frosted elfin is the only elfin species with legal protection (as a threatened species) in Wisconsin (Bureau of Endangered Resources 1999), as well as Michigan, bordering to the east (Nielsen 1999). No elfins are listed in Minnesota, bordering to the west (Cutler et al. 1988, Minnesota Department of Natural Resources 1995).

In this paper, we analyzed the variation in relative abundance and timing of adults of these elfins, as observed in formal surveys and informal visits at numerous sites in Wisconsin during 1987–1999. These analyses included:

- (1) comparisons of the earliest, latest, mean, and median observation dates among four subregions of Wisconsin,
- (2) tabulations of these dates by year in central Wisconsin (the most frequently visited subregion), with tests for significant correlations between span of observation dates and number of individuals recorded within year,
- (3) tests for significant relationships between a species' observation rate (individuals recorded per hour of surveying) with geographical, timing, and weather factors, and
- (4) comparisons of relative abundance among years (i.e., annual fluctuations) at sites surveyed for many consecutive years.

We also sought sympatric butterfly species that might be useful for gauging the phenological progress of the frosted elfin. These analyses should prove useful for designing, implementing, and interpreting surveys to research and monitor populations of these species. In our analyses, we gave particular emphasis to the frosted elfin. As it is the elfin species receiving the most conservation attention in Wisconsin, it would most likely be a particular focus of surveying, which is a necessary component of conservation programs (New 1993, Pollard and Yates 1993). Results for the other elfin species are provided not just as natural history information, but as a context for interpreting results for the frosted elfin. The phenological data for all the elfins also provide a basis for study of possible future climate change (Dennis 1993, Kuchlein and Ellis 1997, Sparks and Yates 1997).

## METHODS

**Field observations.** Since 1986, we conducted formal transect surveys of adult butterflies along similar routes at each site on each visit, as described in Swengel (1996, 1998) and Swengel and Swengel (1996, 1997). These surveys occurred at about 160 Wisconsin pine-oak barrens sampled because of their apparent potential to support barrens-specialized butterflies. These sites represent a diversity of ownerships and land uses, including government or private conservation reserves, government-owned forest reserves for timber harvest, military reservation, and rights-of-way for highways and utility lines. All sites could not be visited each year, but most were visited more than once both within and among years. Most surveys occurred during 1991–1999. Survey times and locations were selected especially to study barrens-specialized butterflies, as classified in Swengel (1998). A high priority was the frosted elfin, of lesser priority was the Henry's elfin, while no priority was given to other elfin species.

Walking at a slow pace (1.5–2 km/hr) on parallel routes 5–10 m apart, we counted all adult butterflies observed ahead and to the sides, to the limit of species identification (possibly with binoculars after detection) and ability to track individuals. Within a barrens site, we designated a new sampling unit (i.e., subsite) whenever the habitat along the route changed by management type and/or year of treatment, canopy, and/or vegetative quality (based on diversity and abundance of native and exotic flora). We tried to avoid double-counting an individual, either within or among units, during a survey at a site. For each unit, we recorded temperature, wind speed, percent cloud cover, percent time sun was shining, route distance, and time spent surveying. Data from each unit were kept separate. Surveys occurred during a wide range of weather conditions and times of day. Occasionally surveys occurred in intermittent light drizzle, so long as butterfly activity was apparent, but not in continuous rain.

We kept records on informal observations of elfins that might occur before/after a formal survey while we were still at the study site or on informal visits to a variety of other sites and habitats in Wisconsin. In these informal observations, sampling did not necessarily follow a set route nor were time (duration) and weather recorded. However, numbers of elfin individuals observed were usually tallied. Butterfly nomenclature follows North American Butterfly Association (1995).

**Dataset assembly.** The dataset included all formal surveys and informal observations recording any elfin(s), identified or not. These elfin localities were grouped into subregions based on county boundaries (Fig. 1). Latitudinally, subregion 3 grouped logically with subregion 4, but we kept subregion 3 separate because the sites visited there had a greater affinity in habitat to sites in 2 than 4. Elfin observations occurred on formal surveys in all four subregions.

We included formal surveys not recording any elfins, if they were within the span of dates in that subregion that year when we observed any elfins. The species total was set as zero (so as to include that survey result in analyses) for an elfin if the survey date occurred within the span of dates that species was observed in that subregion that year. Sometimes we recorded one or a few individuals 1–2 weeks outside the regular span of observation for that species in that subregion that year. In that case, we did not insert zeroes for surveys on dates between those outlier date(s) and the next nearest date of observation that year, as absence on surveys during that period could be attributed to seasonal timing rather than low numbers of the species in the site.



Figure 1. Map showing boundaries of four study subregions in Wisconsin.

In this dataset, the latitudinal ranges for the sites in each subregion were 43.19–43.61, 43.97–44.70, 45.73–46.09, and 45.36–46.86° N, respectively. The longitudinal ranges were 89.73–90.53, 90.12–91.02, 92.11–92.74, and 88.32–92.16° W, respectively. Most sites in subregions 1–3 had sandy soils, while the bogs in subregions 2–3 had peat soils and the remaining sites in subregions 1–2 had silty loess soils (based on Zimmerman 1991). All these soil types, plus heavy clay soil, were represented in the sites of subregion 4.

To document additional opportunities to record elfins that turned out to occur outside the span of dates for our elfin observation in that subregion that year, we included formal surveys before any elfins were observed in that year (as early as 2 April), and after (as late as 11 July). These surveys weren't included in elfin analyses (i.e., species totals were set as no value, not zero), but serve only to define the precision of first and last dates of observation we recorded. If no formal surveys occurred between 2 April and 11 July but outside the span of dates any elfins were observed in that subregion

that year, we included informal visits during that time period, but only if any butterflies of any species were recorded (i.e., demonstrating that it was weather conducive to butterfly observation) and the visit was to a site where we had ever observed elfins.

We sought other sympatric butterfly species that might be useful for gauging the phenological progress of frosted elfin adults, the only elfin with legal conservation status in Wisconsin. We selected olympia marble [*Euchloe olympia* (W. H. Edwards 1871)] and spring larvae and adults of the bivoltine Karner blue (*Lycaeides melissa samuelis* Nabokov 1944), because they are easily detected and identified, widely distributed in frosted elfin habitat, and occur before or overlapping with frosted elfin adults. The Karner blue, federally listed as endangered, is the subject of much surveying in Wisconsin, such that a state-operated telephone hotline provides timely phenological information on this butterfly (Wisconsin Department of Natural Resources 1999). Comparisons occurred only in subregion 2, where all our frosted elfin observations occurred, and during 1992–1999, when we surveyed most often. Phenological events included:

- (1) first date of observation for a 13 mm or larger larva,
- (2) first date for mean 10 mm or larger larvae,
- (3) last date before any adults observed (if <7 days before date of first adult observed),
- (4) first date for adults,
- (5) date for “maximum” adults (highest relative density—i.e., individuals/hour per unit survey—on a single survey),
- (6) date for “peak” adults (highest mean relative density, if >1 site surveyed that date), and
- (7) last date for adults.

Definitions of phenological events and dates for Karner blue events during 1992–1998 follow Swengel and Swengel (1999).

**Statistical analysis.** We calculated first and last observation dates of the season for each species in each subregion for all years pooled (using both formal and informal observations). If we observed the species on more than one date, we calculated median and mean observation dates by weighting each date by the number of individuals observed. For subregion 2, which had the most survey dates, we calculated first, last, median, and mean dates for each species in each year. Spearman rank correlation was used to test for significant relationships between number of days in the observed flight period and total number of individuals observed.

Spearman rank correlation was used to test observation rates (relative densities or abundances) of each study species for patterns relative to:

- (1) geography (latitude and longitude),
- (2) timing (beginning time of survey and crepuscularity—i.e., difference between 1200 hr CST and time when unit survey started), and
- (3) weather (percent time sun was shining, percent cloud cover—i.e., mean of beginning, ending, lowest, and highest percent cloud cover, temperature—i.e., mean of beginning, ending, lowest, and highest temperature, and wind speed—i.e., mean of lowest and highest wind speed).

We calculated observation rates as individuals observed per hour in each formal unit survey. It was necessary to standardize the data as observation rates because the routes varied in length among units. Unit surveys were in-

cluded in an analysis only if held on dates during the species' flight period (i.e., within the span of dates adults of the species were observed in that sub-region that year) at sites within the range of the species recorded during these surveys. Analysis was performed at the scale of the unit rather than by site, because unit surveys within the same site varied, sometimes considerably, in vegetative characteristics and weather. The Mann-Whitney U test was used to test for significant differences in geography, timing, and weather on unit surveys during the elfin's flight period by whether the species was recorded (in any numbers) or not.

We computed all statistics with ABstat 7.20 software (Parker, Colorado, USA). Significance was initially set as a two-tailed  $p < 0.05$ . Since significant results occurred overall at a frequency well above that expected due to spurious Type I statistical error, we did not lower the P value further, as many more Type II errors (biologically meaningful patterns lacking statistical significance) would then be created than Type I errors eliminated.

**Population monitoring.** For species observed in sufficient numbers and years (all except Henry's elfin), we identified sites surveyed formally for the most consecutive years possible where we had ever recorded the elfin species in formal surveying during that period: seven and five monitoring sites, respectively, for brown and hoary elfins during 1993–1999; and nine and ten sites, respectively, for frosted and eastern pine elfins during 1992–1999. We conducted a similar analysis with 17 sites for frosted elfin during 1994–1999. Analysis limited to 1994–1999 did not markedly increase the sample of sites for the other elfins. This analysis was limited to sub-region 2, where we conducted the most surveying, so that our peak counts would most closely correspond to actual peak in the elfins' flight periods.

We identified the peak survey per site per year on formal surveys during flight period. In the few instances when we observed the elfin in the sub-region on only one date in a year and a monitoring site lacked a survey on that date, we used a survey from another date for this analysis, if that date occurred (1) within one week of the single observed date and that single date occurred around the typical median and mean observation dates, (2) within one week after the single observed date if that single date fell near the typical first observation date for that elfin, or (3) within one week prior if that single date fell near the typical last observation for the elfin. This was necessary only for brown elfin (for 8 of 49 surveys; once each for six sites, twice for the seventh site; in 1997 and once in 1998) and hoary elfin (for 3 of 35 surveys, twice for one site, once for another site; once each in 1996, 1997, and 1998).

In comparisons within species of abundance trends and fluctuations among sites and years, the peak survey total (not observation rate per hour) was analyzed, since survey route and length within a site was held constant. For each monitoring site, we calculated the percentage the elfin was recorded as present, both by year (using peak survey) and for all formal surveys during the flight period.

## RESULTS

During 1987–1999, we recorded elfin individual(s) on 154 of 254 observation dates in the study season (Fig. 2), and on 82 of 120 dates in the most frequently visited subregion (Fig. 3). On every date we recorded unidentified elfin(s) in a subregion, other elfin(s) were identified to species. Frosted elfins occurred in only one subregion (2) and eastern pine elfins in all four, while the other species occurred in the three more northern subregions (Table 1).

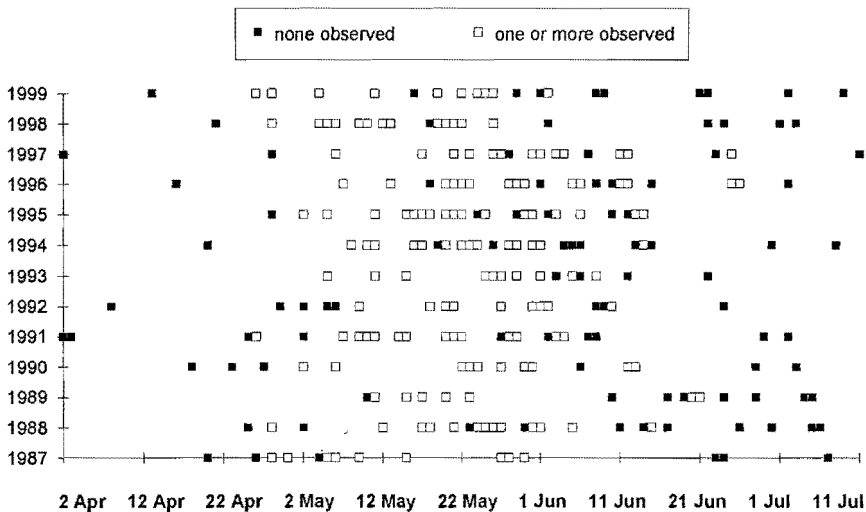


Figure 2. Dates of observation during the study season (2 April–11 July) and study years (1987–1999) in the entire study region (Fig. 1), by whether any elfins (identified to species or not) were observed on that date.

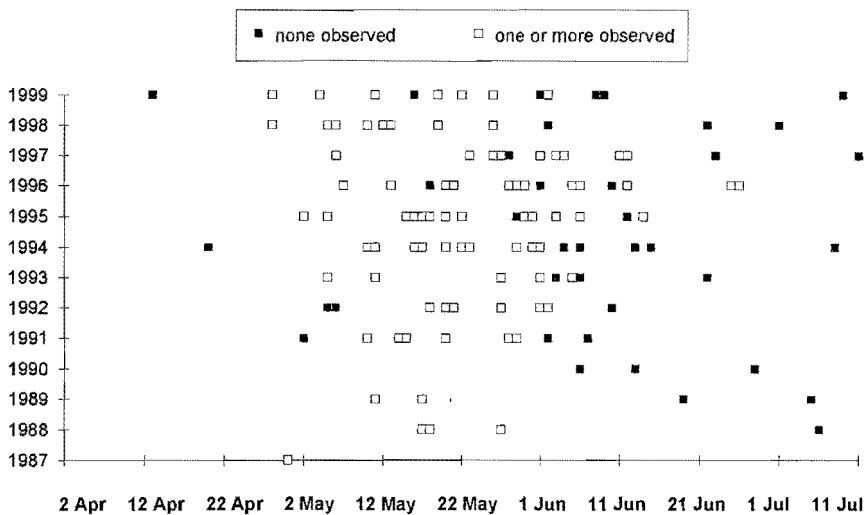


Figure 3. Dates of observation during the study season (2 April–11 July) and study years (1987–1999) in subregion 2 (central Wisconsin) (Fig. 1), by whether any elfins (identified to species or not) were observed on that date.



Most identified individuals were eastern pine elfins, which occurred at the most sites, while Henry's elfin had the fewest individuals and sites (Table 1).

**Elfin flight periods.** Median and mean observation dates tended to occur progressively later the more northerly the subregion, but less so the last dates and not so the first dates (Table 2). Since subregion 3 had the fewest survey dates, with none in June, that subregion should either be disregarded or combined with the latitudinally similar subregion 4 for comparisons among subregions. In the most frequently visited subregion (2), hoary and eastern pine elfins had the earliest observation dates, while frosted elfin was somewhat later in first and last dates than the other elfins except eastern pine elfin, which had the latest date. But within subregion 2 and subregions 3–4, the different elfins had similar median and mean dates.

All elfin observations in subregion 1 occurred in uplands; most in subregions 2–3 did too, but a few were in bogs. In subregion 4, the data were adequate for subdivision by these habitats (Table 2). The first and last dates for brown elfin were later in bogs than uplands, but median and mean dates were similar. All dates for eastern pine elfin were similar between these habitats.

In comparisons between Michigan (Nielsen 1999) and Wisconsin of cumulative elfin flight periods based on decades of records (Table 3), first dates in Michigan were earlier than in Wisconsin except vice versa for Henry's elfin. Recorded flight spans were longer in Michigan than Wisconsin except for Henry's and frosted elfins. In both states, brown and eastern pine elfins had the longest spans, followed by hoary elfin, while frosted and Henry's elfins had the shortest.

In subregion 2, the frequency of survey dates was sufficient to analyze flight periods by year (Tables 4–5). Comparisons among years are more meaningful in 1994–1999, which had more elfin observation dates per year than 1987–1993 (Fig. 3). The number of individuals observed per year often covaried significantly with the span of days between first and last observation dates, and no correlations were significantly negative (Table 6). These correlations were significant when the lowest number of individuals recorded in a year was 0 or 1, but were not significant when >110 individuals were recorded in the sample (except for all elfin species pooled) (cf. Tables 5–6). During 1994–1999, mean flight spans per year were 20, 18, 31, 10, and 36 days for brown, hoary, frosted, Henry's, and eastern pine elfins, respectively—i.e., a mean of 56% (range 38–76%) of the cumulative flight spans for these species over all of those years. During 1994–1999, variability in timing among years differed by type of date (first, last, median, mean) and species (Table 7). The frosted elfin varied least in first and last dates, and brown elfin in median and mean dates. The hoary elfin, which had the most years (3) with single observation dates (Table 4), varied most in timing except eastern pine elfin varied most in first date.

The Highway X powerline corridor had the highest numbers and most consistent observations of frosted elfin (Fig. 4). We observed this species on each visit there within the flight span we recorded for frosted elfin throughout subregion 2 (cf. Fig. 4, Table 4), except for none seen at this corridor in the midst of the flight on 23 May 1994 (in overcast, deteriorating weather), at the end of the flight on 12 June 1995, and at the start of the flight on 6 May 1997. At this corridor, we walk down the ditches on either side of the highway and return by the powerline paralleling the highway to the east. To avoid double-counting, we do not record individuals by the powerline from the ditch or vice versa. Most individuals (126) were by the powerline, and few (21) in the ditches, including dates of highest survey totals: 23 by the powerline and 5 in the ditches (5 May 1998), 29 and 7 (13 May 1998), and 11 and 3

Table 1. Total individuals (total) and number of sites (sites) recorded for each elfin, and total observation dates (total) of any elfin (identified or not), and total number of sites (sites) visited on dates shown in Fig. 2, by subregion (mapped in Fig. 1). The number of dates per subregion sums to >154 because on a few dates, elfins were recorded in more than one subregion.

	Subregion 1		Subregion 2		Subregion 3		Subregion 4 upland		Subregion 4 bog		All subregions	
	total	sites	total	sites	total	sites	total	sites	total	sites	total	sites
Brown elfin			100	26	7	3	85	11	221	16	413	56
Hoary elfin			130	29	26	9	117	6			273	44
Frosted elfin			350	41							350	41
Henry's elfin			15	13	14	6			1	1	30	20
Eastern pine elfin	60	12	341	45	12	1	115	14	7	4	535	76
Unidentified elfin	1		154		5		42		4		206	
Observation dates	31		82		8		29		14		154	
N study sites		13		136		24		22		17		212

Table 2. First and last observation dates of the season for each elfin, and median and mean dates if recorded on >1 day, by subregion, and first and last observation dates (as in Fig. 2) for each subregion.

	Subregion 1	Subregion 2	Subregion 3	Subregion 4 upland	Subregion 4 bog
First-last dates					
Brown		30 Apr–06 Jun	23 May–25 May	26 Apr–20 Jun	21 May–25 Jun
Hoary		28 Apr–06 Jun	28 Apr–25 May	20 May–13 Jun	
Frosted		04 May–14 Jun			
Henry's		04 May–30 May	23 May–26 May		28 May
E. Pine	26 Apr–05 Jun	28 Apr–26 Jun	28 Apr–26 May	28 Apr–14 Jun	28 Apr–13 Jun
Median/mean dates					
Brown		17 May/16 May	25 May/25 May	30 May/28 May	24 May/29 May
Hoary		16 May/17 May	25 May/21 May	23 May/26 May	
Frosted		20 May/20 May			
Henry's		16 May/19 May	24 May/24 May		
E. Pine	11 May/14 May	19 May/20 May	26 May/20 May	24 May/27 May	24 May/22 May
First-last dates					
Observation	2 Apr–7 Jul	13 Apr–11 Jul	28 Apr–26 May	2 Apr–24 Jun	28 Apr–25 Jun

Table 3. Cumulative flight spans based on decades of records for the study species in Michigan and Wisconsin, where the elfins' ranges are similar latitudinally except frosted elfin's recorded range is narrower in Wisconsin than Michigan (Opler 1995, Nielsen 1999).

	Michigan <sup>1</sup>		Wisconsin <sup>2</sup>	
	range	span	range	span
Brown	18 April–16 July	89	26 April–25 June	60
Hoary	3 April–3 June	61	25 April–13 June	49
Frosted	25 April–5 June	41	4 May–14 June	41
Henry's	5 May–6 June	32	26 April–6 June	41
Eastern pine	18 April–11 July	84	26 April–26 June	61

<sup>1</sup>from Nielsen (1999).

<sup>2</sup>from Ebner (1970), Leuschner (1974–1975), Winter (1980–1982), Kuehn (1983), Preston (1983–1991), McKown (1992–1994), Minno and Minno (1995), Tuttle (1996–1999), and Table 2.

(11 May 1999). To guard further against double-counting, on these dates as on the others, we moved past individuals with care and they usually did not flush. Even on 13 May 1998, when we recorded the most individuals ever, we moved easily from one frosted elfin to the next with both remaining in view.

We compared the phenology of the frosted elfin flight period to the timing of olympia marble adults and spring Karner blue larvae and adults (Table 8). During 1992–1999 in subregion 2, we recorded 1753 olympia marbles in formal surveys on 54 dates and 1659 Karner blue adults on 25 dates through the end of the frosted elfin flight period; 485 spring larvae occurred on 46 dates, 346 frosted elfins on 52 dates. The first date for frosted elfin followed that for olympia marble by a mean of +8.6 days (range 0–21). In two years (1994, 1997) of the three when we first observed both species on the same date, no visits occurred in that subregion for 20 days prior, so we were unlikely to have recorded earlier dates for either species. The first date for a mature Karner blue larva ( $\geq 13$  mm in length) preceded that for adult frosted elfin by a mean of –1.0 days (range –7 to +1—i.e., preceding by 0–7 days except following by 1 day in 1995). The first date for an adult Karner blue followed that for frosted elfin by a mean of +14.3 days (range +6–21), and followed frosted elfin peak by a mean of +0.4 days (range –8 to +11). The first date of an adult Karner blue followed the frosted elfin maximum by a mean of +3.0 days (range –6 to +11). The least variable relationship to frosted elfin phenology was the first mature Karner larva (typically before first frosted elfin adult, and bracketing that date by only 8 days). The most consistent phenological markers in terms of sequence were the first olympia marble adult (never following first frosted elfin adult) and first Karner blue adult (always after first frosted elfin adult).

**Weather, timing, geography.** Of the four analyzable species, only frosted elfin showed any significant influences of weather (temperature only) on observed density (Table 9). But we observed frosted elfins in nearly the full range of temperatures occurring on formal surveys in the species' flight period and range (15–32° out of 13–32°C). Likewise, we recorded brown, hoary, and eastern pine elfins in temperatures ranging from 13–16°C to 30–32°C, out of a possible 12–13°C to 30–32°C.

Three of four elfins related significantly and negatively to crepuscularity—i.e., their observed densities increased the nearer to noon (Table 9). The

Table 4. First and last observation dates for each elfin, and median and mean dates if recorded on &gt;1 day, by year in subregion 2.

	Brown elfin	Hoary elfin	Frosted elfin	Henry's elfin	Eastern pine elfin
<b>First-last dates</b>					
1987	30 Apr				
1988	17 May–27 May	17 May–18 May	17 May–18 May	17 May	17 May–27 May
1989	17 May	11 May–17 May			17 May
1990					
1991	10 May–15 May	10 May–15 May	20 May		10 May–29 May
1992	27 May	20 May	20 May–01 Jun		18 May–02 Jun
1993	11 May–01 Jun	05 May–01 Jun	11 May–05 Jun		05 May–01 Jun
1994	10 May–22 May	10 May–31 May	10 May–01 Jun	16 May–17 May	10 May–01 Jun
1995	02 May–31 May	05 May–31 May	15 May–14 Jun	15 May–30 May	05 May–06 Jun
1996	07 May–06 Jun	21 May–06 Jun	20 May–12 Jun	21 May–29 May	07 May–26 Jun
1997	23 May	06 May	06 May–12 Jun		26 May–11 Jun
1998	13 May	28 Apr	05 May–26 May		28 Apr–26 May
1999	04 May–22 May	04 May	04 May–02 Jun	04 May	28 Apr–22 May
All	30 Apr–06 Jun	28 Apr–06 Jun	04 May–14 Jun	04 May–30 May	28 Apr–26 Jun
<b>Median/mean dates</b>					
1987					
1988	17 May/20 May	17 May/17 May	18 May/18 May		17 May/18 May
1989		14 May/14 May			
1990					
1991	14 May/13 May	15 May/13 May			29 May/26 May
1992			27 May/26 May		20 May/22 May
1993	11 May/19 May	01 Jun/23 May	01 Jun/28 May		01 Jun/26 May
1994	14 May/14 May	16 May/15 May	17 May/18 May	17 May/17 May	11 May/17 May
1995	15 May/14 May	17 May/20 May	30 May/26 May	16 May/21 May	17 May/22 May
1996	21 May/20 May	28 May/27 May	29 May/29 May	25 May/25 May	29 May/27 May
1997			03 Jun/02 Jun		03 Jun/04 Jun
1998			13 May/10 May		13 May/11 May
1999	11 May/12 May		11 May/12 May		19 May/15 May
All	17 May/16 May	16 May/17 May	20 May/20 May	16 May/19 May	19 May/20 May

Table 5. Span of observation dates and total individuals recorded for each elfin, by year in subregion 2. During 1994–1999, values are provided for years when we recorded no individuals of an elfin because survey dates were sufficiently frequent and broadly timed (Fig. 3) for that elfin's flight period likely to be covered anyway.

	Brown elfin		Hoary elfin		Frosted elfin		Henry's elfin		Eastern pine elfin	
	span	total	span	total	span	total	span	total	span	total
1987	0	2								
1988	10	12	1	7	1	2	0	1	10	10
1989	0	8	6	2					0	3
1990										
1991	5	6	5	3	0	2			19	40
1992	0	4	0	5	12	13			15	36
1993	21	5	27	3	25	10			27	21
1994	12	16	21	65	22	38	1	2	22	72
1995	29	23	26	35	30	99	15	9	32	29
1996	30	17	16	6	23	33	8	2	50	33
1997	0	1	0	2	37	26	0	0	16	15
1998	0	1	0	1	21	84	0	0	28	41
1999	18	5	0	1	29	43	0	1	24	6
1987–1999	37	100	39	130	41	350	26	15	59	339
1994–1999	35	63	39	110	41	323	26	14	59	196

Table 6. Coefficients (r) and P values for Spearman rank correlations between span of observation dates and total elfin individuals recorded in a year during 1994–1999 in subregion 2, by individual years and for all years pooled (as in Table 5). N = number of separate years x number of species in correlation; ns = not significant.

	N	r	P value
All years individually			
Brown elfin	6	+0.882	<0.05
Hoary elfin	6	+0.893	<0.05
Frosted elfin	6	−0.257	ns
Henry's elfin	6	+0.938	<0.01
Eastern pine elfin	6	+0.143	ns
All five elfin species	30	+0.789	<0.01
All years pooled			
All five elfin species	5	+0.900	<0.05

Table 7. Variation among years (difference in days) in first, last, median, and mean observation dates (Table 4) for each elfin in subregion 2 during 1994–1999. When a species was recorded on only one date in a year, that date counts as beginning, end, median, and mean date.

Date	Brown elfin	Hoary elfin	Frosted elfin	Henry's elfin	Eastern pine elfin
First	21	23	16	17	28
Last	24	39	19	26	35
Median	12	30	23	21	23
Mean	11	29	23	21	24

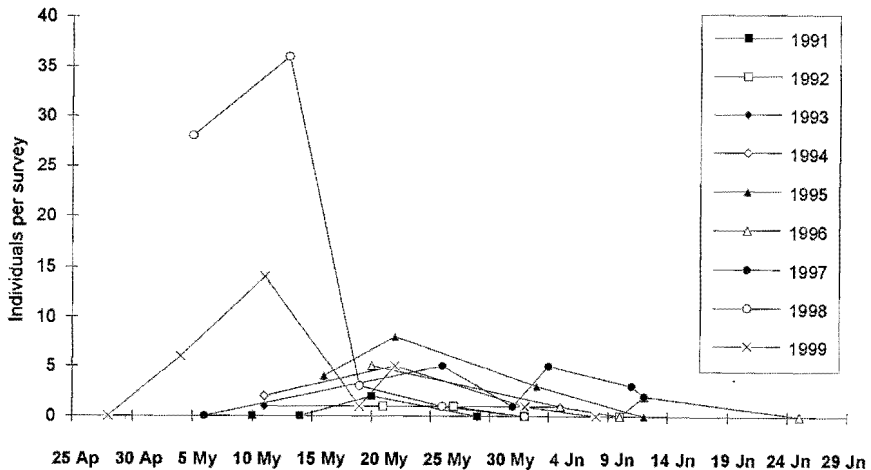


Figure 4. Frosted elfin flight period recorded each year at Highway X, based on 147 recorded individuals (143 on formal surveys, 4 informally—either before/after formal survey or on a visit of casual observation only) seen on 27 of 46 dates for visits during the study period.

eastern pine elfin also correlated significantly and negatively with increasing time of day. Nonetheless, the frosted elfin was observed in a wide range of timings (0710–1750 hrs CST), nearly the entire range possible (0649–1812 hrs), as was hoary elfin (0714–1715 out of 0649–1715 hrs). We recorded brown elfin during 0753–1530 hrs (out of a possible 0649–1715 hrs) and eastern pine elfin during 0714–1618 hrs (out of a possible 0649–1715 hrs).

Three of four species (except eastern pine elfin) covaried significantly with increasing latitude (Table 9), including frosted elfin, which occurred only in subregion 2 in a rather narrow latitudinal range (Table 1). Hoary elfin also covaried significantly with longitude (Table 9).

Identical patterns of whether a test was significant, and in what direction, occurred in Mann-Whitney U tests for differences in weather, timing, and geography between unit surveys with the species recorded as present or not.

**Population monitoring.** All four analyzable elfins fluctuated markedly in abundance among years, based on the mean of peak survey totals at the same sites per year (Figs. 5–7). These elfins all had a relatively high mean in 1994 and low means in 1996 and 1997. Brown and hoary elfins were most similar in fluctuations and were the only species pair (in all combinations of values in Figs. 5–7) to correlate significantly in annual means (Spearman rank  $r=+0.806$ ,  $n=7$  years,  $p<0.05$ ).

These peak survey totals varied little among years and sites for two elfins (0–5 individuals for brown and 0–4 for hoary elfins), but one site each for frosted and eastern pine elfins had much higher peak survey totals than the other sites (Table 10). These “outlier” sites had by far their highest survey totals in 1998 (Figs. 6–7), and with these outlier sites included, both elfins had their highest annual means that year. But excluding the outlier

Table 8. Dates (MDD; e.g., 426 = April 26) of phenological events for olympia marble, frosted elfin, and spring Karner blue adults, and spring Karner blue larvae, in subregion 2 for each year during 1992–1999.

	Olympia marble			Frosted elfin						Karner blue			
	none <sup>1</sup>	first <sup>2</sup>	last <sup>3</sup>	none <sup>1</sup>	first <sup>2</sup>	peak <sup>4</sup>	max. <sup>5</sup>	last <sup>3</sup>	none <sup>6</sup>	13 <sup>7</sup>	10 <sup>8</sup>	none <sup>1</sup>	first <sup>2</sup>
1992		505	528	506,518	520	601	601	601	602,610	518	518	521	526
1993	505	511	605	505	511	605	601	605	606,622	511	519	527	601
1994		510	601		510	517	517	601	604,606,613	510	510	520	522
1995	426	502	606	505,509	515	530	522	614		516	516	530	531
1996		507	606	507,513	520	528	528	612	625,626	520	520	530	601
1997		506	612		506	604	526	612	623	506	506	526	527
1998		428	513	428	505	513	513	526	602,622	428	506	512	513
1999		413	526	413,428	504	511	511	602	608	504		519	522

<sup>1</sup>Last date no adults were observed prior to the first date adults were observed, based only on visits to sites where the species was ever recorded.

<sup>2</sup>First date adults were observed.

<sup>3</sup>Last date adults were observed.

<sup>4</sup>Date with highest mean relative density (individuals/hour per unit survey), if >1 site surveyed that date.

<sup>5</sup>Date with highest relative density on a single survey.

<sup>6</sup>First date no adults were observed after the last date adults were observed, based only on visits to sites where the species was ever recorded.

<sup>7</sup>First date 13 mm or larger spring larva was observed.

<sup>8</sup>First date with mean of 10 mm or larger for spring larvae, if >1 larva observed that date.

Table 9. Spearman rank correlation coefficients of relative density (individuals/hr, per unit survey) with geography, timing, and weather factors, with \* for  $p < 0.05$  and \*\* for  $p < 0.01$ .  $N = 546, 482, 713$ , and  $899$  unit surveys, respectively, during the elfin species' flight period in all subregions in range.

	Brown elfin	Hoary elfin	Frosted elfin	Eastern pine elfin
Geography				
Latitude	+0.153**	+0.212**	+0.148**	-0.031
Longitude	+0.008	+0.228**	+0.035	-0.005
Timing				
Crepuscularity <sup>1</sup>	-0.130**	-0.044	-0.113**	-0.156**
Time of day	-0.063	+0.016	+0.044	-0.098**
Weather				
Percent cloud cover	+0.005	-0.046	-0.062	-0.059
Percent sunshine	+0.008	+0.070	+0.040	+0.011
Temperature	-0.029	-0.054	+0.083*	-0.026
Wind speed	+0.026	-0.007	+0.015	+0.011

<sup>1</sup>Number of hours from noon CST. A higher number is more crepuscular (i.e., nearer to sunrise/sunset).

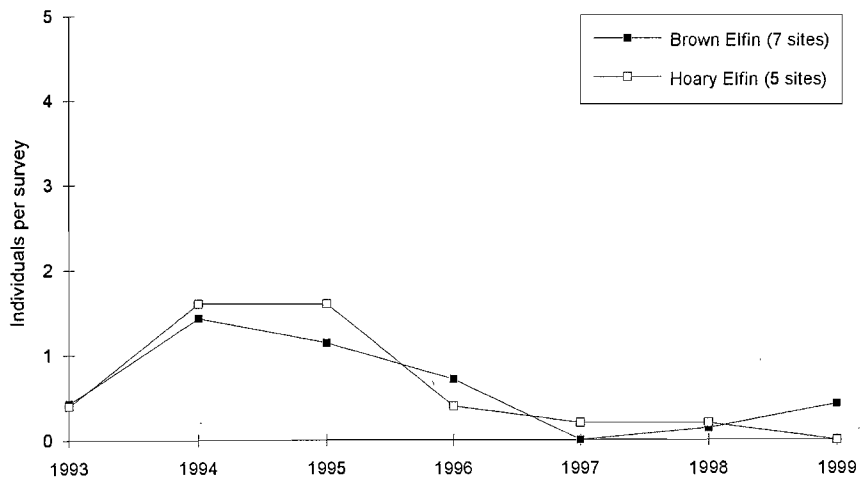


Figure 5. Mean survey totals for brown and hoary elfins on the peak survey per site each year during 1993–1999 in subregion 2 (Fig. 1). For each species, all analyzed sites had recorded the species in at least one of the analyzed years and had been surveyed each year in the species' flight period.



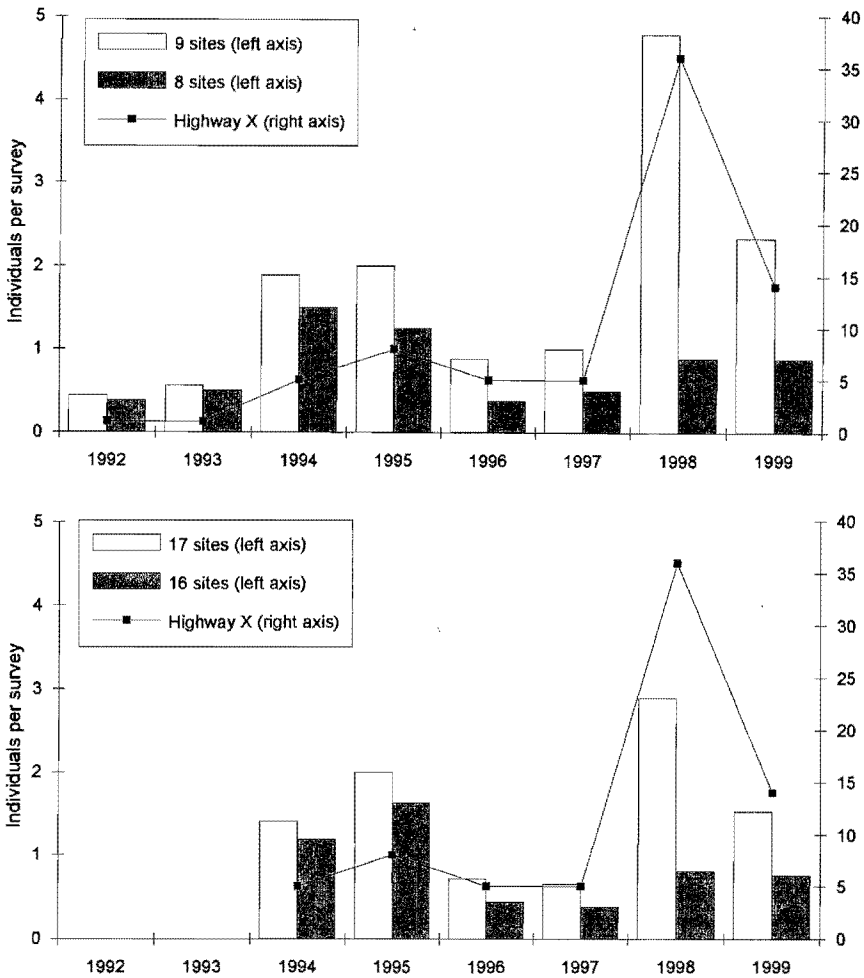


Figure 6. Mean survey totals for frosted elfin on the peak survey per site each year in subregion 2 (Fig. 1), both as all sites and as all sites except for the outlier site (Highway X, Table 10), which is presented separately. All analyzed sites had recorded the species in at least one of the analyzed years. Nine sites (top) and 17 sites (bottom) were surveyed each year in the species' flight period during 1992–1999 and 1994–1999, respectively.

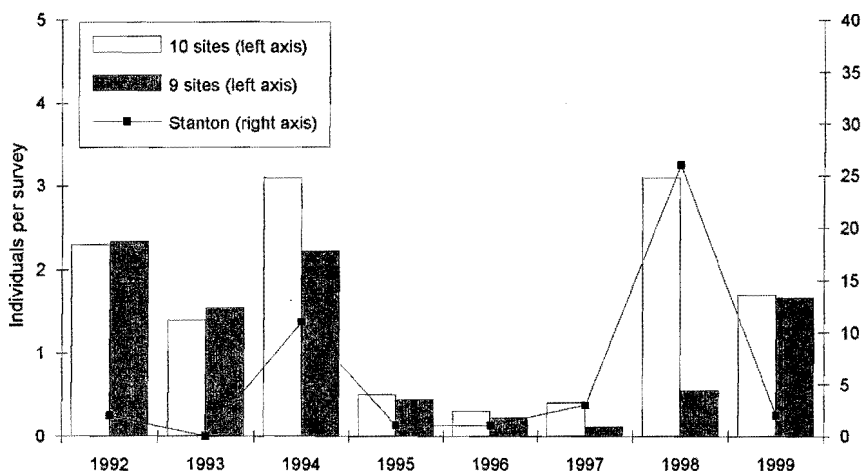


Figure 7. Mean survey totals for eastern pine elfin on the peak survey per site each year during 1992–1999 in subregion 2 (Fig. 1), both as all sites and as all sites except for the outlier site (Stanton, Table 10), which is presented separately. All analyzed sites had recorded the species in at least one of the analyzed years and had been surveyed each year in the species' flight period.

Table 10. Variation among years in peak survey totals, as analyzed for population monitoring of frosted and eastern pine elfins (Figs. 6–7), between the outlier site with the highest survey total and the other sites. Outlier sites had the highest relative density (individuals/hr).

	Outlier site		Other sites	
	mean	range	mean	range
Frosted elfin, 1992–1999	9.4	1–36	0.8	0–7
Frosted elfin, 1994–1999	12.2	5–36	0.9	0–7
Eastern pine elfin, 1992–1999	5.8	0–26	1.1	0–16

sites, these elfins' annual means in 1998 were much lower than in two or more other years. For both frosted and eastern pine elfins, peak survey totals at the outlier site did not relate significantly in Spearman rank correlations with the annual means for the other sites.

We calculated annual means for frosted elfin both for 9 sites during 1992–1999 and 17 sites during 1994–1999. Annual means for these two groups of sites covaried significantly (Spearman rank correlation  $r = +0.886$  including outlier site and  $r = +0.870$  excluding it;  $n = 6$  years,  $p < 0.05$ ).

For the sites analyzed from 1992 or 1993 through 1999, the proportion of sites with any individual(s) of the species recorded on the peak survey was similarly low for all analyzed elfins in 1993 and high in 1994 (Fig. 8). Otherwise these proportions were desynchronized among years, and no species pairs related significantly in Spearman rank correlations. Within species,

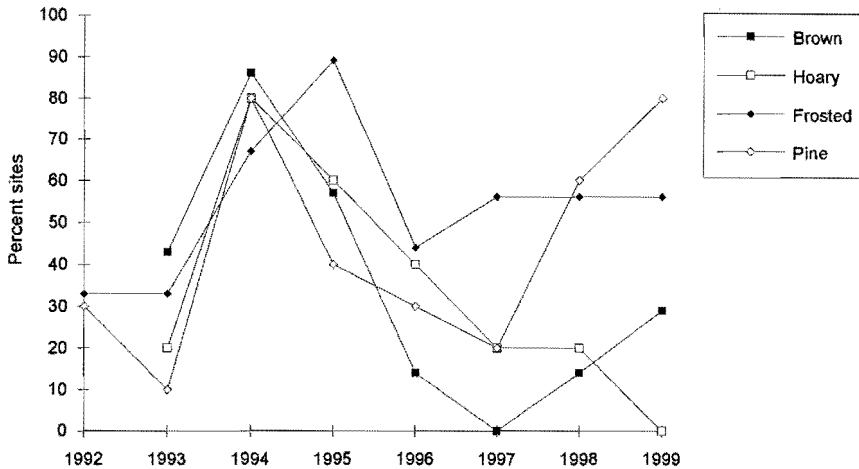


Figure 8. Percent of peak surveys each year with the elfin species recorded as present at sites analyzed for population monitoring from 1992 or 1993 through 1999 (Figs. 5–7), by year.

this presence/absence proportion did covary significantly in Spearman rank correlations with the annual mean of peak survey totals (cf. Fig. 8 to Figs. 5–7) for brown, hoary, and frosted elfins (for this last species, both including or excluding outlier site), but not for eastern pine elfin. For both frosted and eastern pine elfins, the outlier site (as described in Table 10) had the highest rate of presence on peak surveys and all surveys.

For brown, hoary, and eastern pine elfins, the proportion of peak surveys recording the species per year was <50% in more than half the years (Fig. 8). In the majority of years, the median of the peak survey totals was 0. For frosted elfin, with the outlier site included (as in Fig. 8), this proportion was <50% in three years and >50% in five years (median always 1). Excluding the outlier site, this proportion was <50% in three years, at 50% in three (with a median of 0.5 individuals—this being the mean between 0 and 1 as necessitated by the even number of sites analyzed), and >50% in two (median always 1). For all analyzed elfins (with or without outlier sites), positive medians were usually 1 and never >2. Use of the median would alleviate skewing of the mean annual index by the outlier site in the outlier year, but at great loss of resolution, since the medians reduced the analysis nearly to presence/absence, with absence usually occurring in more years than presence.

When these sites were ordered by the proportion of years any individual(s) of the species were recorded in the peak survey, slopes were fairly linear (Fig. 9), with brown very similar to hoary elfin, and frosted to eastern pine elfin. For the proportion of all surveys during the species' flight period with any individual(s) recorded, all four elfins had similar curvilinear declines (Fig. 10).

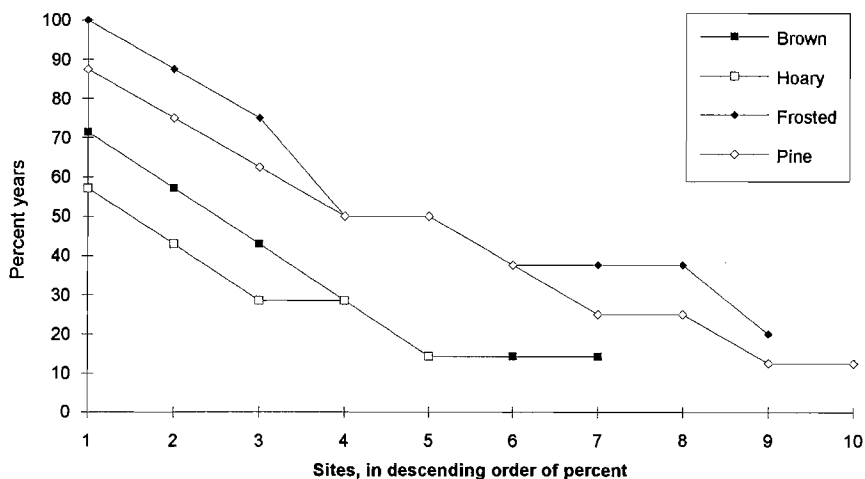


Figure 9. Percent years each elfin was recorded as present on the peak surveys at each site analyzed for population monitoring from 1992 or 1993 through 1999 (Figs. 5–7), in descending order of percent.

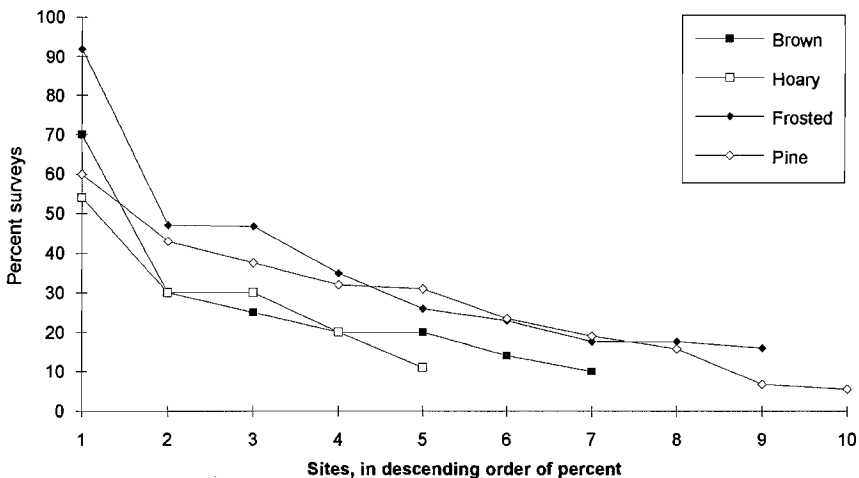


Figure 10. Percent surveys each elfin was recorded as present on the peak surveys at each site analyzed for population monitoring from 1992 or 1993 through 1999 (Figs. 5–7), in descending order of percent.

## DISCUSSION

Since the study sites in subregion 2 were strongly biased toward frosted elfin habitat (areas with wild lupine, the larval host), the relative abundance of frosted elfins in this study, compared to brown, hoary, and eastern pine elfins, is not representative of their distribution and abundance in that subregion overall. The latter three elfins often occurred in frosted elfin localities, but also in a variety of sites lacking lupine. Thus, the more localized occurrence of the frosted elfin, relative to these three elfins, is not readily apparent from summary statistics of our results (Table 1). Henry's elfin also occurred in non-lupine sites, but very few were recorded anywhere in this study. It is unclear whether we would have encountered more Henry's elfins if we had surveyed other places, but it is highly likely we would have recorded brown, hoary, and/or eastern pine elfins in additional sites (bogs, pine plantations, sandy uplands lacking lupine) had we visited them.

Detectability also affects the relationship between numbers seen and actually present. We observed all the study species flying upward out of sight, particularly in interactions with other elfin(s), but it is our impression that the species with herbaceous or short shrubby hosts (brown, hoary, and frosted elfins) seemed more often to perch below eye level and engage in horizontal flight. It is unclear what host(s) Henry's elfin uses in Wisconsin, but it and eastern pine elfin (tree host) readily flew skyward when disturbed. We observed all the study species to engage in rapid flight we could not track, but frosted elfins tended to be most sedentary and short and slow in flight (Swengel 1996). All these factors would make the frosted elfin relatively more detectable than the other elfins.

**Elfin flight periods.** Comparisons of these elfins' cumulative flight spans between Michigan and Wisconsin (Table 3) suggest that, with more records in more years, the span for Henry's elfin in Michigan will likely increase, as should those for brown, hoary, and eastern pine elfins in Wisconsin. Despite the eastern pine elfin being the most widespread and abundant elfin in Wisconsin (Ebner 1970, Opler 1995, this study), the fewest records were available for determining its cumulative flight span, since Ebner (1970) described its flight period without precise dates and records for this common species are rarely published (Leuschner 1974–1975, Winter 1980–1982, Preston 1983–1991, McKown 1992–1994, Minno and Minno 1995, Tuttle 1996–1999). By contrast, Nielsen (1999) determined Michigan flight spans for all the elfins based on decades of records. Thus, the longer spans reported for more elfins in Michigan than Wisconsin (Table 3) agree with the positive correlation of number of observed individuals with flight spans in this study (Table 6). However, for individual species, a threshold seemed to occur above which additional recorded individuals did not contribute significantly to an increased flight span in a given year (Table 6). This limit is likely reached more quickly within a given year because of the constraints of phenology on flight period. When pooling records from many years, the very wide range of phenologies allows a much larger cumulative span than observed in a single year (Table 4).

For all elfin study species, the mean and median observation dates in the earliest year(s) occurred before the first observation date in the latest year(s) (Table 4). Even the long-term mean and median dates occurred before the first date in the latest year(s) for all species except all these dates were the same for frosted elfin (Table 4). Despite considerable dissociation among years in flight periods, they did overlap at least some in most years. During 1994–1999, the flight periods of the four analyzable elfins in individual years averaged about half the cumulative flight span for all those years. Since

flight spans for butterflies are often reported as first and last dates from a pool of years (e.g., Glassberg 1999, Nielsen 1999), these percents provide some indication of how much of that span a flight period is likely to cover in a given year.

In contrast to the considerable phenological variation between the Karner blue and gypsy moth (*Lymantria dispar* L.) (Herms et al. 1997), frosted elfin phenology corresponded to that for olympia marble and Karner blue rather consistently (Table 8), especially given the approximate dating in this study since we could not sample every day or every other. To obtain and apply these phenological markers in future surveys, a pool of sites should be sampled, since a single site may have low numbers of these other butterflies in those year(s). Based on a pool of sites, olympia marble adults, and then mature Karner blue larvae, appear before frosted elfin adults, and the first spring Karner blue adult indicates that the frosted elfin flight period is around peak or maximum by about  $\pm 1$  week. These phenological markers would be particularly useful in surveys for frosted elfins at sites where few (if any) may be seen, as it still appears possible to validate the appropriate time for fielding surveys.

**Weather, timing, geography.** Analyses indicated virtually no significant effects of weather on observed densities of the four analyzed elfins (Table 9), and we recorded them in broad ranges of weather conditions. Three elfins significantly related to time of day, especially nearness to noon (Table 9), although all were detected in a wide range of daily timing. Three elfins significantly related to latitude and/or longitude within their Wisconsin range. Thus, it appears that location within range and daily timing, as well as flight period timing (discussed above) are more important for elfin detection than weather, within the broad range of conditions in which any butterfly activity is apparent.

**Population monitoring.** In a few years, abundance was higher or lower for elfins generally (Fig. 8), but only brown and hoary elfins correlated significantly with each other in annual fluctuations. Thus, the elfins' marked annual fluctuations (Figs. 5–7) were desynchronized for most species-pairs. Some desynchronization also occurred within species, based on non-correlation of annual indices between the outlier and other sites for frosted and eastern pine elfins (Figs. 6–7; see Results). An outlier site experiencing an outbreak year can heavily influence the mean annual index, which would then become a less accurate representation of the annual fluctuation for the pool of sites.

For frosted elfin, nearly doubling the pool of sites from nine to 17 did not markedly alter the analysis of annual fluctuation, since their mean annual indices covaried significantly. This implies that the smaller pool was sufficient to characterize annual fluctuations. However, this was a narrow analysis. All sites had ever recorded the species during the period of analysis and we recorded presence at slightly more than half the sites in >50% of the years. If these proportions were lower, a larger number of sites would be necessary. Moreover, to obtain the sample of sites used in the analysis, we actually conducted consistent surveying at additional sites of plausible habitat where we failed to record frosted elfin. Since this analysis only covered six years, we did not address turnover (extirpation and founding of populations), which is an important element of long-term population monitoring. A sample of nine sites would likely be inadequate for robust population monitoring over the long term, especially for a rare species with typically low density populations, volatile flight period timing and abundance, and potential population turnover.

At only one monitoring site for one species (Highway X for frosted elfin)

was the species recorded as present in each year we monitored, although the frosted elfin was the elfin we most concentrated on finding each year (by focusing site selection in subregion 2 on frosted elfin habitat). While all monitoring sites had at least one record of the elfin species being monitored, some sites may not have supported regularly resident populations of the species. But other sites likely did, yet with frequent observations of the species at these sites, we still did not record the species there each year, much less on each survey during the species' main flight period. The percent sites where the species was recorded as present covaried significantly with that year's annual mean of the peak survey totals (Figs. 5–7) for most analyzed elfins. This indicates that the ability to document presence of an elfin relates to the species' abundance (annual fluctuation) that year.

**Summary.** Since elfin abundance and phenology vary considerably among years, the appropriate time for detecting these species' adults must be determined individually for each year. For the frosted elfin, it was especially valuable to survey the Highway X corridor often within and among years, as this was our most reliable site for observing this species. Given the fewer and more erratic observations at the other sites, we could have become discouraged and ceased surveying them before the flight period was over, although we sometimes obtained the survey with peak (or any) numbers at these sites late in the flight period. With the intensity of surveying and types of populations sampled here, our results indicate that it is unlikely an elfin species will be recorded each year even at sites where resident populations likely occur consistently. In the last few years, we recorded some elfin species only on one date in all of subregion 2, although we visited a number of sites with regular occurrence of species throughout the season of its cumulative flight span. Since the ability to demonstrate presence of these elfins varies among years due to variation in annual abundance and flight period length, assessments of their status and abundance cannot be reliably based on surveys at only a few sites or in a few years.

#### ACKNOWLEDGMENTS

We gratefully acknowledge funding for some field surveys from the U.S. Fish and Wildlife Service and the Wisconsin Department of Natural Resources in 1990–1994 and 1996, and from Drs. William and Elsa Boyce in 1994–1995 and 1997–1998. We thank Judi Maxwell for touring the senior author around Fort McCoy and finding the first frosted elfin there. Likewise, Necedah National Wildlife Refuge staff have kindly permitted access to closed areas. We appreciate the numerous useful comments on the manuscript by M. C. Nielsen and an anonymous reviewer.

#### LITERATURE CITED

- Bureau of Endangered Resources. 1999. The endangered and threatened invertebrates of Wisconsin. PUB-ER-085-99. Wisc. Dept. of Nat. Resources, Madison. 80 pp.
- Cutler, B., R. Dana, R. Huber, R. Bright and L. Pfannmuller. 1988. Invertebrates, pp. 375–431. *In*: B. Coffin, and L. Pfannmuller (eds.), Minnesota's endangered flora and fauna. Univ. Minnesota Press, Minneapolis. 473 pp.
- Dennis, R. L. H. 1993. Butterflies and climate change. Manchester Univ. Press, Manchester, U.K. 302 pp.
- Dirig, R. 1994. Historical notes on wild lupine and the Karner blue butterfly at the Albany Pine Bush, New York, pp. 23–36. *In*: D. A. Andow, R. J. Baker and C. P. Lane

- (eds.), Karner blue butterfly: a symbol of a vanishing landscape. Misc. Publ. 84—1994, Minn. Agric. Exp. Sta., Univ. Minnesota, St. Paul. 222 pp.
- Ebner, J. A. 1970. The butterflies of Wisconsin. Milwaukee Public Museum, Milwaukee. 205 pp.
- Gatrelle, R. R. 1991. The taxonomic implications of the discovery of *Incisalia irus* in Florida. News Lepid. Soc., No. 4 Jul./Aug. 1991: 57–58.
- Glassberg, J. 1999. Butterflies through binoculars: the East. Oxford Univ. Press, New York. 242 pp.
- Hermes, C. P., D. G. McCullough, L. S. Bauer, R. A. Haack, D. L. Miller and N. R. Dubois. 1997. Susceptibility of the endangered Karner blue butterfly (Lepidoptera: Lycaenidae) to *Bacillus thuringiensis* var. *kurstaki* used for gypsy moth suppression in Michigan. Great Lakes Entomol. 30: 125–141.
- Kuchlein, J. H. and W. N. Ellis. 1997. Climate-induced changes in the microlepidoptera fauna of the Netherlands and the implications for nature conservation. J. Insect Conserv. 1: 73–80.
- Kuehn, R. M. 1983. New Wisconsin butterfly records. J. Lepid. Soc. 37: 228–35.
- Leuschner, R. 1974–1975. Season summary. News Lepid. Society, No. 2.
- McKown, S. 1992–1994. Season summary. News Lepid. Society, No. 2.
- Minnesota Department of Natural Resources. 1995. Proposed amendment of Minnesota rules, chapter 6134: endangered and threatened species, butterflies and moths. Dec. 4, 1995: pp. 117–133.
- Minno, M. C. and M. F. Minno. 1995. Season summary. News Lepid. Society, No. 2.
- North American Butterfly Association. 1995. Checklist & English names of North American butterflies. North American Butterfly Association, Morristown, NJ. 43 pp.
- New, T. R. 1993. Introduction to the biology and conservation of the Lycaenidae, pp. 1–21. In: New, T. R. (ed.), Conservation biology of Lycaenidae (butterflies). IUCN, Gland, Switzerland. 173 pp.
- Nielsen, M. C. 1999. Michigan butterflies & skippers: a field guide and reference. Mich. State Univ. Ext., East Lansing. 248 pp.
- Opler, P. A. 1995. Lepidoptera of North America. 2. Distribution of the butterflies (Papilionoidea and Hesperioidea) of the eastern United States. C. P. Gillette Museum of Insect Biodiversity, Fort Collins, CO. 6 pp. + unnumbered pp.
- Opler, P. A. and G. O. Krizek. 1984. Butterflies east of the Great Plains. Johns Hopkins Univ. Press, Baltimore. 294 pp.
- Pollard, E. and T. Yates. 1993. Monitoring butterflies for ecology and conservation. Chapman & Hall, London. 274 pp.
- Preston, J. 1983–1991. Season summary. News Lepid. Society, No. 2.
- Schweitzer, D. F. 1992. *Incisalia irus* revisited: a response to Reverend Ronald Gatrelle. News Lepid. Soc., No. 4: 69–70.
- Scott, J. A. 1986. The butterflies of North America. Stanford Univ. Press, Stanford, CA. 583 pp.
- Sparks, T. H. and T. J. Yates. 1997. The effect of spring temperature on the appearance dates of British butterflies, 1883–1993. Ecography 20: 368–374.
- Swengel, A. B. 1996. Observations of *Incisalia irus* (Lepidoptera: Lycaenidae) in central Wisconsin, 1988–95. Great Lakes Entomol. 29: 47–62.
- Swengel, A. B. 1998. Effects of management on butterfly abundance in tallgrass prairie and pine barrens. Biol. Conserv. 83: 77–89.
- Swengel, A. B. and S. R. Swengel. 1996. Factors affecting abundance of adult Karner blues (*Lycaeides melissa samuelis*) (Lepidoptera: Lycaenidae) in Wisconsin surveys 1987–95. Great Lakes Entomol. 29:93–105.
- Swengel, A. B. and S. R. Swengel. 1997. Co-occurrence of prairie and barrens butterflies: applications to ecosystem conservation. J. Insect Conserv. 1: 131–144.
- Swengel, A. B. and S. R. Swengel. 1999. Timing of Karner Blue (Lepidoptera: Lycaenidae) larvae in spring and adults in spring and summer in Wisconsin during 1991–98. Great Lakes Entomol. 32: 79–95.



- Tuttle, J. 1996–1999. Season summary. *News Lepid. Society*, No. 2 (1996–1998), Suppl. S1 (1999).
- Winter, D. 1980–1982. Season summary. *News Lepid. Society*, No. 2.
- Wisconsin Department of Natural Resources. 1999. Wisconsin Statewide Karner Blue Butterfly Habitat Conservation Plan and Environmental Impact Statement, Vol. 3, Appendix G. Effectiveness Monitoring Protocol. Wisconsin Dept. Nat. Res., Madison. pp. G-1 to G-14.
- Zimmerman, J. H. 1991. The landscape and the birds, pp. 35–90. *In*: S. D. Robbins (ed.), Wisconsin birdlife: population & distribution past & present. Univ. Wisconsin Press, Madison. 702 pp.